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On the Locomotor and Feeding Behavior of Certain Postlarval Clupeoidea.

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(Plates I & II; Text-figures 1-3).

Introduction.

In connection with studies on the life history of the Tarpon being carried on at the laboratory of the New York Aquarium, located on Palmetto Key, Florida, it became necessary to handle and examine all other isospondylous fishes living in that vicinity. Their larval stages were given considerable attention. In connection with this work it was found possible to establish in laboratory aquaria the postlarvae of both *Anchoa mitchilli* (Cuvier and Valenciennes)[1] and *Harengula pensacolae* Goode and Bean.[2] The feeding behavior and locomotor habits of the very delicate juveniles of these species were studied in some detail and found to show certain noteworthy characteristic features. These studies were undertaken by both authors in the summer of 1940 and continued by the senior author during the summers of 1941 and 1942. We are grateful to Dr. Carl L. Hubbs for various critical remarks on some of the items contained herein.

Locomotor Behavior.

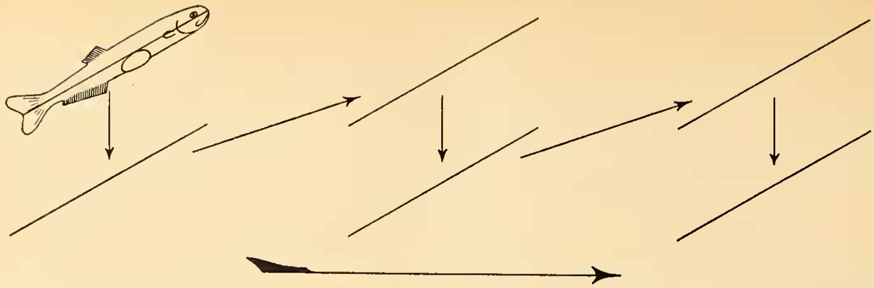
The postlarvae of *Anchoa mitchilli* must exert mechanical forces in order to maintain their position at a given depth of water and to maintain their equilibrium. Active and apparently normal postlarvae that had become well established in aquaria were clearly seen to sink when they ceased active swimming. On sickening or on the slightest shock they turned over and sank, ventral side up. Despite their rather large swim bladder, they evidently are slightly heavier than sea water. The position of the swim bladder, below the center of gravity, is obviously an important factor in this unstable equilibrium. Although, as pointed out by Lochhead (1942), the ballistics of a dead or disorganized fish cannot be used for determining their normal hydrostatic or hydrodynamic characteristics, it is at least suggestive.

When not actively feeding, the postlarvae of *A. mitchilli* are usually inclined upward and forward at an angle of about 30° to the horizontal. In this position they sink for about one-half their length and then swim directly forward, thus regaining their former position in regard to depth of water and coming to rest in advance of their original location at a distance about equal to one and a half times their own length. They then sink and repeat the locomotor performance again and again. This gives them a forward translation interrupted by sinking movements about as indicated in Text-figure 1. These postlarvae exhibit strong schooling tendencies and this mode of progression is most frequently seen in a broad, quietly milling school.

The specific gravity of the adult anchovies seems to be closer to that of the sea water, but they are evidently still a little heavier than the surrounding medium, for they show a bare suggestion of similar correction, by swimming efforts, of a tendency to sink. Superficially the tendency to turn over is not evident in sound specimens, either adult or postlarvae, but the pectoral fins are seen to be in constant irregular motion, as though beating down to correct an ever-so-slight roll, that cannot be otherwise detected. The adults, like the postlarvae, sink back-down when about to expire. Fin-clipping or other methods of direct approach are not

[1] According to Hildebrand (1943) all the material found in the vicinity of this station is referable to the race *A. m. diaphana* Hildebrand. He discusses the situation in considerable detail.

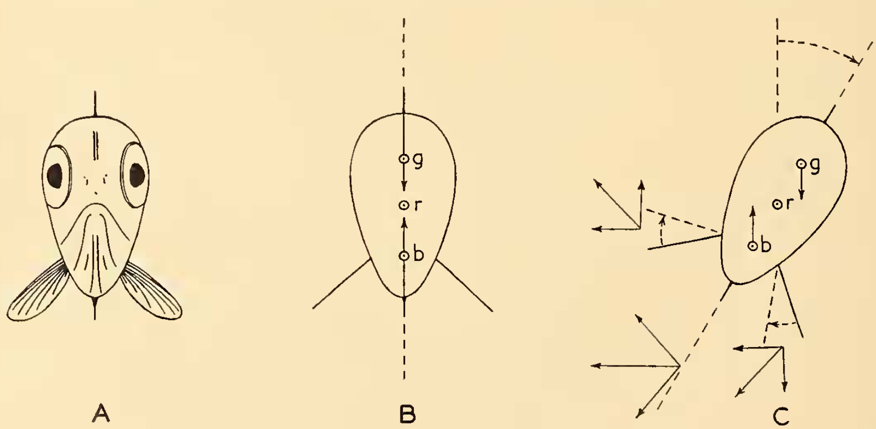
[2] According to Storey (1938) this name, rather than *H. macrophthalma* (Ranzani) as used by Breder (1942 b), is applicable to the form found in this locality.



TEXT-FIG. 1. Swimming movements of larval anchovy, indicating extent of sinking and extent of foward and upward swimming. The fish figure is represented at the end of each successive sinking and swimming period of an axial line, the arrows indicating the direction of translation.

practicable in these exceedingly fragile fishes, for even the most gentle handling produces the disturbances described above. Conversely, when large numbers are handled, a few individuals do survive tow-net operations and can be established in aquaria.

As nearly as can be interpreted from simple observation, the anti-roll mechanism works about as follows. The apparent activity of the pectoral fins is indicated in Text-figure 2 in which "A" shows a front view of a mature anchovy with the pectorals in the position they take as they beat irregularly on each side. Careful and repeated checking indicates that what actually takes place is something like that shown in the rest of Text-figure 2. In "B" is shown a body like that of *Anchoa* with "g," the center of gravity, higher than "b," the center of buoyancy, respectively above and below "r," the center of roll. The pectoral fins, when thrust out as indicated in "A," form, even when they are at rest, an impediment to the rolling couple inherent in the positions of "g" and "b." When rolling once starts as indicated in "C" it is corrected by quick movements of the right and left pectorals in opposite directions, as indicated. That is, in a roll to the right, the right fin beats down and the left up. The fins are then immediately folded close to the body and then thrust out in the position shown in "B." It will be noted that position "B" makes them equally available for checking a roll to either side. It is these movements of the fins that can be detected and are what have been previously referred to as irregular. It must be borne in mind, however, that these movements are very slight and rapid and not easy to see. They are exaggerated in the diagrams shown in Text-figure 2. Vector diagrams in "C" indicate the components of each pectoral and their resultant as well as their combined values as a reaction force against the vertical center of the fish. For further analyses of such vectors see Breder (1926) and Breder and Edgerton (1942) and for other considera-



TEXT-FIG. 2. Equilibrium maintenance in *Anchoa mitchilli*. **A.** Front view of fish, showing disposition of pectoral fins at rest; diagrammatic. **B.** Front view of a body such as an anchovy in unstable equilibrium. **g**—center of gravity. **b**—center of buoyancy. **r**—center of roll. **C.** Dynamic checking of an incipient roll by action of the pectoral fins. Lettering as in "B." See text for full explanation.

tions on the role of the paired fins in reference to equilibrium see Harris (1936, 1937, 1938).

Between these correcting movements there is an intermittent simultaneous down beating of the pectorals which lifts the head for swimming upward and forward, as indicated in Text-figure 1. It may also be that these fish are slightly head-heavy as in the downward sinking of a weakened or dead specimen the head tends to lead the tail, but this may be due to the streamlined form and its consequent tendency to orientation.

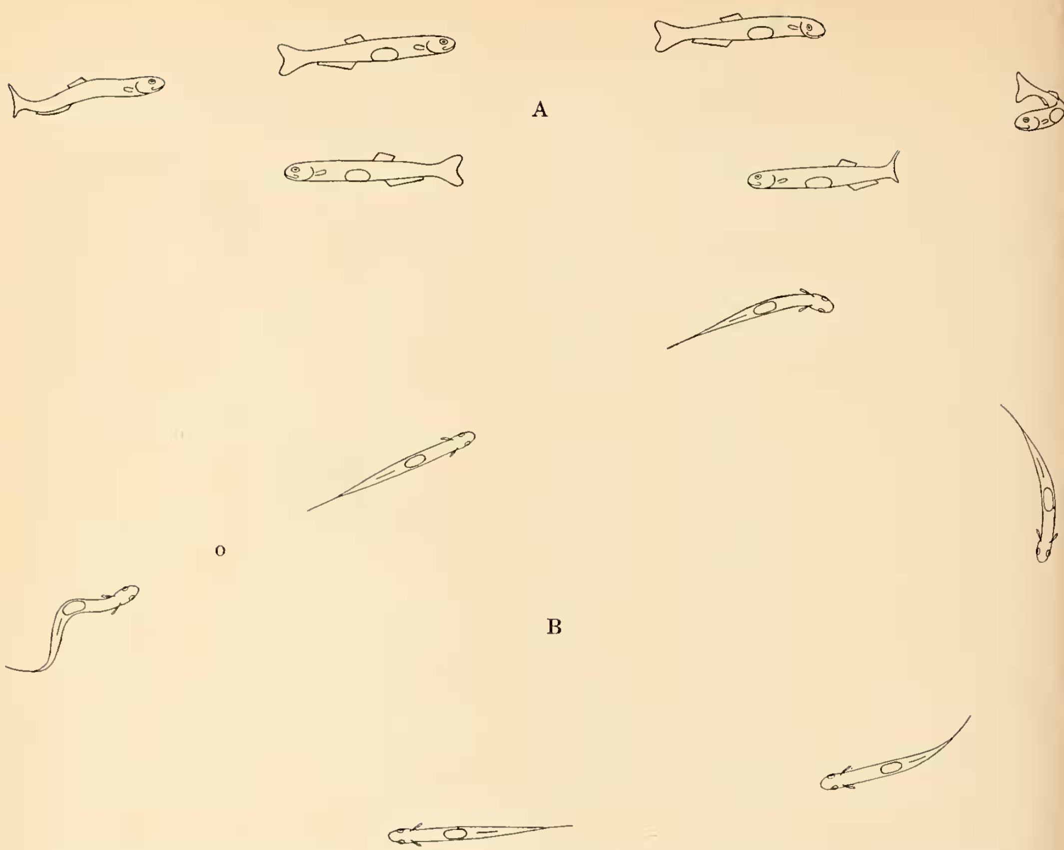
The swimming of these fishes agrees well with the method of sinking and swimming by jerks as discussed by Lochhead (1942) who gives an excellent discussion of the hydrodynamics involved. Normally these fish do a considerable amount of chasing about in the open sea but on very wide flats of shallow water the schools often attain a fairly quiescent state in the vicinity of pilings. Similar reactions are seen in aquaria and are presumably associated with a restricted volume of water. Incidentally one of the specimens had a copepod attached to its dorsum. This fish, which may be seen vaguely in Plate II, Fig. 6, had completely compensated for this added material and could not be separated from its fellows on a basis of behavior. It must be borne in mind that the above-discussed corrections of tendencies to sink as well as that to roll over are maintained in the face of several continually varying factors. For example, every bit of food ingested, the progress of digestion and the voiding of excrement alters the delicate balance between the values of "g" and "b" and shifts their position fore and aft. Such observations have a direct bearing on the work of Lochhead (1942) in that they refer his concepts to an immediate minute to minute basis.

In *Tarpon atlanticus* respiratory gulps influence buoyancy, as may be seen from their tendency to sink and the associated fin movements of the pectorals, which are not unlike those described for the very much smaller anchovy. Observations in an aquarium of tarpon ranging from about 6 to 100 cm. indicate that they seem to become heavier as the time for them to rise for breath approaches. Their pectorals typically work harder and finally with a burst of tail effort they rush to the surface and gulp. It may be that in clear, well-oxygenated water this is what actually triggers off the impulse to rise and gulp. After the ingestion of air they are usually lighter than water and frequently have difficulty descending until they emit small bubbles by way of the gill clefts, after which they reach a state of approximate balance and from then on become heavier again. It would seem that this increase in specific gravity is associated with the fact that their gills are also functional and that there would seem to be a progressive loss of buoyancy by the branchial elimination of CO_2. For further details on the respiratory rises in the Tarpon see Shlaifer and Breder (1940), Shlaifer (1941) and Breder (1942 a).

The comments made above apply to *Harengula pensacolae* quite as well as to *Anchoa mitchilli*. The physical differences and similaries of the two species is evident in Plate II. Even after it has reached the adult form, *Harengula* clearly shows the intermittent sinking as diagrammed in Text-figure 1. A photograph of a small school of these fish of about 30 mm. in standard length is given in Plate I. The angles of five fish, that are clearly side on, are 22°, 33.5°, 32.5°, 32.5° and 40°, with a mean of 32.1°, in reference to the horizontal as indicated by the frame of the aquarium in the background. This mean angle is very close to the estimate of 30° for the postlarvae of *Anchoa*. The photograph was taken just as most of the fish had reached the bottom of their sinking movement. It will be noted that they not only all head nearly in the same direction but that they are mostly in closely similar stages in regard to the sinking-swimming movements. A young *Mugil cephalus*, otherwise alone, had attempted to school with the herrings and is seen in front of one of them. This species does not take on the sinking-swimming type of movement, at this size at least, and its attempts to school with the herrings were eventually given up. The school formation was disrupted by darkness, for its basis is clearly visual, as in most fishes (Newman, 1876; Parr, 1927; Breder, 1929; Spooner, 1931; Bowen, 1931, 1932; Breder and Nigrelli, 1935; and Schlaifer, 1942).

Feeding Behavior.

The approach of the postlarval anchovies and their manner of address to an intended food item is most striking, and is more marked in the smaller and more leptocephalus-like individuals. They do not simply swim up to a planktonic bit of food and ingulf it as might be expected. In these reactions they contrast with most fishes of similar size and state of development that are more customarily kept under conditions permitting close observation of feeding habits. Postlarval anchovies about 15 to 20 mm. long, as seen swimming, appear to be rather stiff-bodied little creatures. Instead of merely darting at the food object, they follow it for a time in a typical stalking approach. Finally they orient themselves in such a position as to "point" it, at which time they draw themselves into a more or less S-shaped form with the head pointing straight at the object. As soon as this "stance" is established the fish straightens



TEXT-FIG. 3. The feeding strike of *Anchoa mitchilli.* **A.** Lateral view of successive positions of the poise for striking and the follow through. **B.** Dorsal view of the same positions. See text for full explanation.

itself out with extreme rapidity, springs forward by the impetus and ingulfs the food. There is a "follow through" of a long sweeping curve that terminates in the normal stiff-bodied swimming attitude. The sequence of these attitudes as seen from the side and from above is shown in Text-figure 3. Plate II shows a variety of poses of these fish, Figure 6 showing the extreme of the S-shaped flexure. The approach to the food item was always made from at least slightly below. In this connection it should be mentioned that in tow-net drags made in the daytime these fish were always found to be much more abundant in samples taken near the bottom rather than in surface tows. Only on dark nights could they be taken in any quantity at the surface. It may be that these fish are accustomed to look up while feeding, silhouetting the plankton against the surface light. The fact that these fish rose to the surface in the sea on dark nights might be associated with a negative phototaxis, daylight merely holding them down. A bright light above an aquarium would force them to a lower level.

As the fish increase in size and gradually transform into juveniles they give up this behavior and substitute for it the usual fish habit of darting at food. Frequently, however, they lapse into a more or less typical postlarval behavior pattern.

The relatively shorter and deeper bodied postlarvae of *Harengula* perform in as similar a manner as their physical attributes permit. Such a fish in its less emphasized "S" striking stance is shown in Plate II, Fig. 8. By the time they have reached the size shown in Plate I such behavior is given up and would likely be impossible because of the increasing stiffness and thickness of the body.

The juvenile pattern of food taking, as here described, certainly seems unnecessary. The food objects, plankton of various kinds, move so slowly as compared with the activities of the much larger fry, that a "pounce" of any kind seems ridiculous. In fact it might be likened to a small boy getting into a certain "striking" position to pick up a slowly walking box turtle. Furthermore these plankton organisms were never seen to make any avoiding reactions to a fish passing near, and if such were made they would surely be ineffectual. Most of the food organisms taken were crustaceans, of the many kinds in which the local waters abound. The fish were noted at times to approach but pass by planktonic forms of relatively moderate size, but which were still too small to make successful avoiding reactions. This behavior was noted as the postlarvae fed, thrived and grew, on such plankton material as was brought to them, mostly by replenishing the sea water in the standing aquaria. Some of these fishes were successfully shipped to the old New York Aquarium and here the same reactions were observed to be successful on newly hatched *Artemia*, a form which they never encountered in the sea, strengthening the view that this behavior is in no way an accommodation to any particular type of organism.

Discussion.

The mechanical features of maintenance of equilibrium by these postlarval fishes is sufficiently evident, but the reasons for the reactions involved are not clear. The relative merits of solid stability and a delicate instability, as discussed by Lochhead (1942), would seem to be the only current view that could be expected to lead to a thorough understanding of this situation. The sinking-swimming movements would seem to be of an adequate magnitude to easily permit of a proprioceptional control of the kind he visualizes. At least these fishes hold their level in an aquarium at night, as was repeatedly demonstrated by flashing a light.

It is difficult to imagine that the peculiar feeding behavior has any particular value in the open sea to fishes that are so much faster than the relatively inert planktonic forms on which they feed. If, on the other hand, one considers the history and relationships of these fishes certain suggestions appear. Since many of the Isospondyli and Apodes agree in having leptocephalus or leptocephaloid postlarvae, the resemblances in the postlarval forms suggest a community of origin, which, as Gregory (1933) indicates, helps reinforce various osteological evidence. He writes, ". . . the 'leptocephalus' larvae of the eels is very similar to that of the isospondyle *Albula*, while the skull of eels seems to be merely a highly specialized derivative of some large-mouthed Cretaceous isospondyle type. *Thrissopater* (A. S. Woodward, 1909) might be such a form, except that the supraoccipital is in contact with the frontals, while in the eels it is separated from them by the parietals. The recent *Engraulis* among the clupeoids shows that the hyomandibular may easily become secondarily directed backward."

In connection with the present discussion an examination of the feeding behavior of the postlarvae of apodal fishes should be of interest. Apparently no such study has been made. Dean (1912) described the swimming behavior on the part of an eel leptocephalus, but unfortunately nothing of its feeding habits. Actually the striking of larval anchovies reminds one strongly of the striking of an adult moray. This in itself may be entirely mechanical; the sea snakes also strike in this fashion. This is in fact, about the only way in which an eel or caudally compressed snake-like form can make a sudden dart when floating freely. In the case of the postlarvae under discussion, however, it should be emphasized that they are not to be thought of as eel or snake-like in length; they are much too short-bodied to derive any special benefit from this eel-like behavior. Actually a more typical fish strike would seem to be just as serviceable to them.

Instability of equilibrium is widespread in the Isospondyli, as is indicated by the reference to adult tarpon, and is apparently a very old feature. For this reason it does not seem likely that this feature of the Isospondyli can be of much significance in such a consideration of the bearing of phylogeny on habits.

It may be that there is some connection between this type of instability and the feeding habits described, an item suggested by Dr. Hubbs. If this is the case, for the reasons already outlined, the mechanical connection between the two features is certainly not evident from any of the data as yet at hand. Very likely both items are widespread among the Isospondyles. Hubbs (1941) points out that a variety of unrelated fishes have independently developed postlarvae which are similarly sub-leptocephaloid in appearance. It would be of interest to compare the feeding behavior and stability characteristics of the postlarval Isospondyles, Apodes and those scattered through other groups. Until something of this nature is undertaken little can be done to separate the items of physical necessity from those of heritage.

Summary.

1. Postlarval *Anchoa mitchilli* and *Harengula pensacolae* are in unstable equilibrium because the center of gravity is higher than the center of buoyancy, while the fishes as a whole are slightly heavier than the water they inhabit.
2. Equilibrium is maintained by mechanical efforts of chiefly the pectoral fins and locomotion proceeds by an alternating series of sinking and swimming periods.
3. These features largely but not com-

pletely disappear as the adult form is reached.

4. These postlarvae feed on small plankton organisms which they stalk and strike in an eel or snake-like manner, a procedure apparently quite unnecessary to catch the relatively inert planktonic particles.
5. This feature of feeding disappears as the adult form is reached.
6. The instability of Isospondyles is widespread and the behavior of the young in this regard is too generalized to be useful at present in understanding relationships.

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EXPLANATION OF THE PLATES

Plate I.

Fig. 1. A group of *Harengula pensacolae* in a typical schooling formation. Most of the fish have just about reached the bottom of a sinking movement and show the typical angle at which they hold themselves. A *Mugil cephalus* which has temporarily joined the school is to be seen just left of center in front of one of the herrings.

Plate II.

Fig. 2. Dorsal view of a larval *Anchoa mitchilli* against a light background. Actually the fish under such conditions is even less visible than appears in the photograph. Usually about all that can be seen under such conditions are the black eyes. Here the centrally located swim bladder can be discerned.

Fig. 3. A pose similar to that of Figure 2 but with the fish showing about the greatest flexure of the body to be seen under ordinary swimming activity.

Fig. 4. A lateral view of *Anchoa mitchilli* indicating a typical pose with reference to the horizontal. The light spot behind the eye is caused by an argenteous layer catching the light and showing through the transparent skin.

Fig. 5. A ventral view of *Anchoa mitchilli*. The interruption of the dark line indicates the position of the ventral fins.

Fig. 6. The typical striking pose at about its greatest point of flexure, just before the fish straightens out and lunges forward. The fish in the background has a parasitic copepod attached near its dorsal fin.

Fig. 7. Another view of *Anchoa mitchilli* striking. Here the fish is partly straightened out as it lunges forward.

Fig. 8. *Harengula pensacolae* partly arched for striking. This fish is of a size nearly ready to abandon the habit. The rather large particle at which it is preparing to strike may be seen not quite a head's length beyond its snout.

Fig. 9. *Anchoa mitchilli* photographed against some verticals and including the water level surface of the aquarium. This represents the steepest angle from the horizontal that these fishes ordinarily reach.